

Article

New *Iguanodon bernissartensis* Axial Bones (Dinosauria, Ornithopoda) from the Early Cretaceous of Morella, Spain

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Abstract: *Iguanodon bernissartensis* is the most frequently and widely cited styracosternan ornithopod in Western Europe during the Early Cretaceous, although some of these assignments likely need to be revised to establish the true distribution of the taxon. Here, we describe a new specimen of *I. bernissartensis* from the upper Barremian of the Iberian Peninsula. Based on the unique combination of shared characters, the new specimen from the Arcillas de Morella Formation at Morella locality (Castellón, Spain) can be confidently referred to *Iguanodon bernissartensis*. These characters include parallel-sided anterior and posterior margins of the dorsal and the caudal neural spines as well as the presence of a ventral keel in the posterior dorsal centra and a broad ventral sulcus in the midline of the central surface of the most posterior sacral vertebrae. This new evidence of *Iguanodon bernissartensis* reinforces the knowledge about styracosternan ornithopods as the most frequently recorded dinosaur group in the Arcillas de Morella Formation.



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Keywords: Styracosterna; *Iguanodon bernissartensis*; Early Cretaceous; Iberian Peninsula; Morella

1. Introduction

Iguanodon bernissartensis Boulenger in [1] is the best represented large Early Cretaceous styracosternan dinosaur in the European “Wealden facies”, and its remains have been frequently found on the Iberian Peninsula. Most of the known material comes from the Maestrazgo Basin (Northeast Spain) and particularly from the Morella sub-basin. The first report on the presence of *Iguanodon* remains in the area of Morella (Castellón province, Spain) was in 1873 [2,3].

However, it was not until 1982 when a partial skeleton discovered in the Mas de Romeu site was described as the first reliable evidence of *Iguanodon bernissartensis* in the Iberian Peninsula [4]. Since then, several partial skeletons have been reported in the late Barremian Arcillas de Morella Formation [5–10], mostly discovered in different sites in the Mas de la Parreta Quarry. In addition to *Iguanodon bernissartensis*, styracosternan fauna from the Arcillas de Morella Formation is composed of *Mantellisaurus atherfieldensis* and *Morelladon beltrani* [9,11].

Recently, a second species of *Iguanodon*, *Iguanodon galvensis*, was described in outcrops of the Galve sub-basin of the Maestrazgo Basin to include several partial skeletons of perinates to sub-adult/adult individuals from the lower Barremian Camarillas Formation close to the locality of Galve (Teruel province, Spain) [10,12–15]. Here, a new specimen of *I. bernissartensis* found in the area named Mas de Sabaté within the Mas de la Parreta Quarry at Morella is described (Figure 1). The specimen consists of a partial skeleton composed of three dorsal vertebrae, a nearly complete sacrum, four caudal vertebrae, several haemal arches, and fragments of dorsal or sacral neural spines. Despite its fragmentary nature, the

specimen can be confidently referred to *I. bernissartensis* based on a unique combination of shared characters.

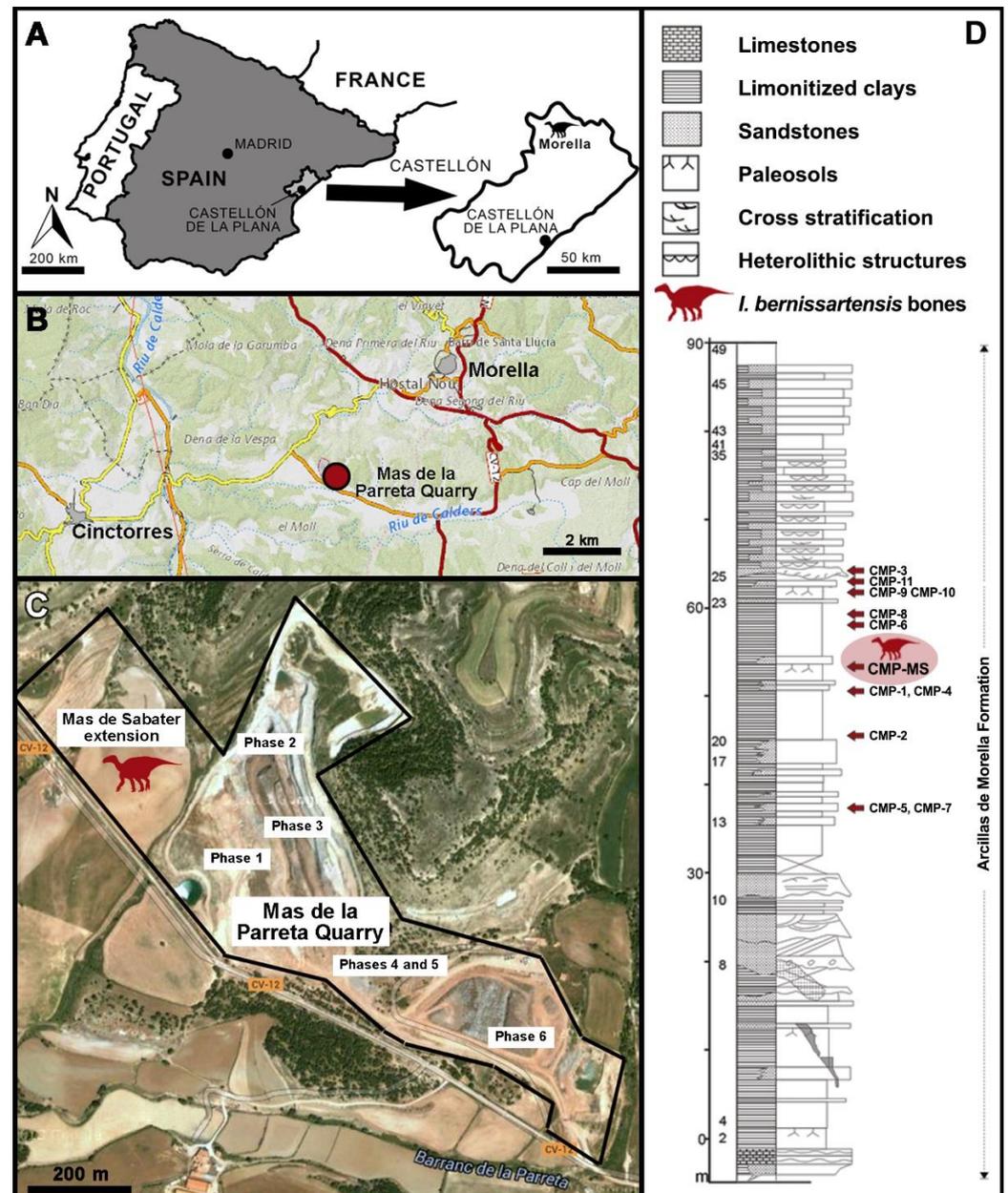


Figure 1. Geographic location of the specimen CMP-MS-04. (A) Castellón province and Morella locality in Spain; (B) Schematic regional map of area of Morella locality indicating location of the Mas de la Parreta Quarry (red circle) (modified from Visor Cartografic de la Generalitat: <https://visor.gva.es/visor/>, accessed on 24 October 2021); (C) Aerial photograph showing the site in which the specimen CMP-MS-04 was located (Mas de Sabater extension) within Mas de la Parreta Quarry (modified from Google Maps: <https://www.google.es/maps/>, accessed on 24 October 2021); (D) Simplified stratigraphic column from the exploitation of the quarry showing the distribution of sedimentary environments and the location of CMP fossil sites including CMP-MS area (light red oval). Phases 1–6 represent distinct extractive clay activities at Mas de la Parreta Quarry by Vega del Moll S.A. company.

Institutional abbreviations: CMP, Mas de la Parreta Quarry, Morella, Spain; DS, Las Dehesillas site, Aliaga, Spain (material housed in the Museo Aragonés de Paleontología, Teruel, Spain); IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

2. Materials and Methods

The locality of specimen CMP-MS-04 was discovered in May 2015 during the paleontological control of the Mas de Sabaté site within the Mas de la Parreta Quarry at Morella (Spain) under permits obtained from the Dirección General de Cultura y Patrimonio [Conselleria de Educació, Investigació, Cultura y Deporte-Generalitat Valenciana (2014/1073-Cs)].

The specimen described here is housed at the Museu Temps de Dinosaurios-Museus de Morella (Morella, Castellón), a part of the Museums Survey of the Generalitat Valenciana. The preparation of the fossil remains was made at the IVCR+i (Institut Valencià de Conservació, Restauració i Investigació) laboratory placed in the locality of Morella, according to the criteria established by the Dirección General de Cultura y Patrimonio of the Generalitat Valenciana.

Here, we compare the anatomy of the fossil bones of the specimen CMP-MS-04 to that of other Early Cretaceous styracosternans dinosaurs described in the literature (e.g., *Iguanodon* species, *Mantellisaurus*, *Morelladon*, and *Barilium*).

3. Results

3.1. Systematic Paleontology

Dinosauria Owen, 1842 [16]

Ornithischia Seeley, 1887 [17]

Ornithopoda Marsh, 1881 [18]

Iguanodontia Dollo, 1888 [19] sensu Norman, 2015 [20]

Ankylopollexia Sereno, 1986 [21] sensu Norman, 2015 [20]

Styracosterna Sereno, 1986 [21] sensu Norman, 2015 [20]

Iguanodon Mantell, 1825 [22]

Iguanodon bernissartensis Boulenger in Van Beneden, 1881 [1]

Holotype specimen: IRSNB R51 (Specimen 1534), an almost complete articulated skeleton.

Referred specimen: CMP-MS-04, a partial skeleton consisting of an incomplete mid-dorsal vertebra, two incomplete posterior dorsal vertebrae, fragment of a dorsal or sacral neural spine, incomplete sacrum, three almost complete anterior caudal vertebrae, a mid-posterior caudal centrum and seven incomplete haemal arches (Figures 2–5) (see Table 1 for measurements).

Comments. CMP-MS-04 can be referred to *Iguanodon bernissartensis* on the basis of a unique combination of characters including parallel-sided anterior and posterior margins of the dorsal and caudal neural spines, the presence of a keel in the ventral surface of the centra in posterior dorsals and a broad ventral sulcus in the midline of the central surface of the most posterior sacral vertebrae.

Locality and horizon. Specimen collected at the Mas de Sabaté (CMP-MS) site within the Mas de la Parreta Quarry at about 4 km to the southwest of the Morella locality in the Els Ports region (Castellon province, Spain). Neither taphonomic studies nor field map accompanied the works, but the remains were collected associated in an area of approximately 4 m². According to both strontium-isotope stratigraphy and ammonite biostratigraphy the Arcillas de Morella Formation is late Barremian in age [23].

Table 1. Measurements (in mm) of the axial elements of the specimen of *Iguanodon bernissartensis* CMP-MS-04. Abbreviations: AAFH: Anterior articular facet height; AAFW: Anterior articular facet width; CL: Centrum length; MAL: Maximum anteroposterior length; PAFH: Posterior articular facet height; PAFW: Posterior articular facet width; PL: Proximodistal length; TL: Length (total).

	CL	AAFW	AAFH	PAFW	PAFH
Dorsal vertebra CMP-MS-04-02	90	135	130	160	135
Dorsal vertebra CMP-MS-04-06	85	140	140	163	145
Dorsal vertebra CMP-MS-04-08	95	107	130	110	127
TL					
Sacrum	850				
	CL	AAFW	AAFH	PAFW	PAFH
Caudal vertebra CMP-MS-04-03	95	115	110	105	110
Caudal vertebra CMP-MS-04-04	95	123	95	100	103
Caudal vertebra CMP-MS-04-05	93	83	88	80	83
Caudal vertebra CMP-MS-04-07	90	120	105	117	125
	PL	MAL			
Chevron CMP-MS-04-09	320	70			
Chevron CMP-MS-04-010	290	75			

3.2. Description and Comparisons

3.2.1. Dorsal Vertebrae

Three incomplete dorsal vertebrae (CMP-MS-04-02, -06, and -08) and a fragment of a dorsal neural spine (CMP-MS-04-18) are preserved (Figure 2).

The most anterior of the preserved dorsal vertebrae is a mid-dorsal (CMP-MS-04-08) (Figure 2A–C). The centrum retains slight opisthocoely, and it is taller than it is wide. The centrum is anteroposteriorly compressed with thickened and transversely expanded rims. The anterior articular facet is flat, whereas the posterior articular facet is concave. Both articular facets are almost oval in profile, and thus the centrum is higher than it is wide. Nevertheless, the dorsal rim related to the floor of the neural canal is nearly straight in the anterior articular facet, whereas it is slightly indented in the posterior articular facet. A thick and rounded midline ventral keel is present.

Both anteriorly and posteriorly the neural canal is large and circular. The transverse processes are broken but they show an elliptical cross-section. The prezygapophyses are slightly extended beyond the anterior margin of the centrum. The oval facets of the prezygapophyses are ventromedially directed forming an angle of 105 degrees between them. Ventrally the margins of the prezygapophyses are clearly separated. The postzygapophyses are located at the base of the neural spine and slightly below to the posterodorsal margin of the transverse processes.

The postzygapophyses extend beyond the posterior margin of the centrum. The articular facets of the postzygapophyses are ventromedially directed and oval-shaped. Both postzygapophyses are separated by a small and deep spinopostzygapophyseal fossa (spof). The preserved portion of the neural spine is anteroposteriorly expanded and transversely flattened. The anterior margin of the neural spine is sharp-edge, whereas the posterior margin is somewhat thicker. The neural spine is slightly posteriorly inclined.

CMP-MS-04-02 (Figure 2D–F) is a nearly complete posterior dorsal vertebra that likely represents the d15 based on comparisons with *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* [24,25] and its shape and the centrum proportion. The centrum is moderately opisthocoelous and anteroposteriorly compressed with thickened rims. The lateral surfaces of the centrum are anteroposteriorly concave and some nutrient foramina are present. The ventral surface bears a subtle and narrow midline keel. Both articular facets are almost circular with the dorsal rim related to the floor of the neural canal indented. The posterior articular facet is slightly transversely wider than the anterior articular facet.

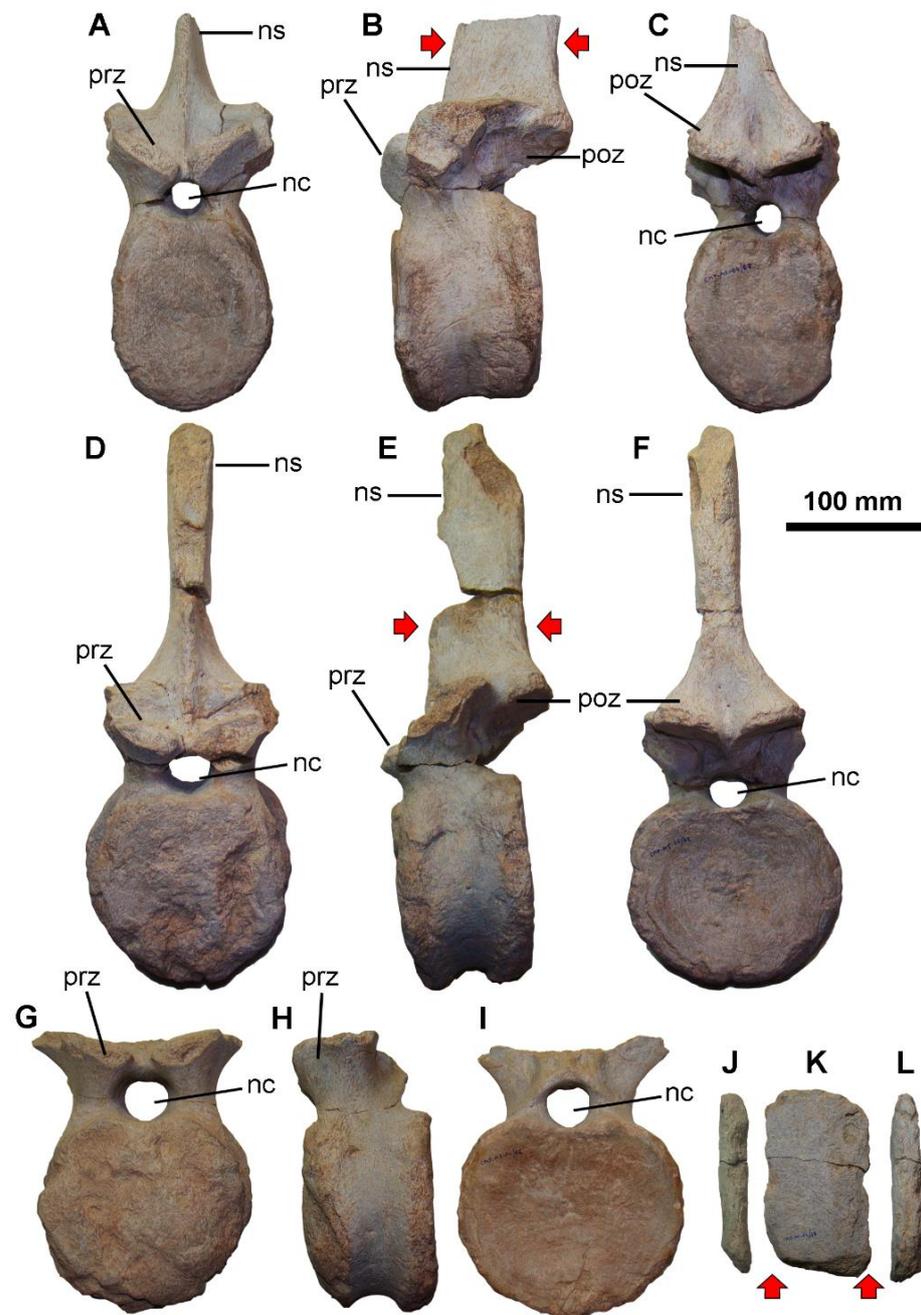


Figure 2. Dorsal vertebrae and partial dorsal neural spine of the specimen CMP-MS-04. CMP-MS-04/08 in anterior (A), left lateral, (B), and posterior (C) views. CMP-MS-04/02 in anterior (D), left lateral, (E), and posterior (F) views. CMP-MS-04/06 in anterior (G), left lateral, (H), and posterior (I) views. CMP-MS-04/18 in anterior (J), lateral, (K), and posterior (L) views. Abbreviations: nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. Red arrows mark the distinctive character that assigned the specimen CMP-MS-04 to *Iguanodon bernissartensis*.

The neural arch is low, robust with the neural canal almost circular and similar in size both anteriorly and posteriorly. The transverse processes are broken and only their bases are preserved. In lateral view, the preserved portion of the transverse processes are anteroventrally directed. The incomplete prezygapophyses are ventromedially directed forming an angle of approximately 145 degrees between them. A groove separates the prezygapophyses from the midline. At the base of the neural spine are the postzygapophyses.

The articular oval facets of the postzygapophyses are large and nearly horizontal. A shallow sulcus extending to mid length of the preserved spine separates the postzy-

gapophyses. The incomplete neural spine is anteroposteriorly expanded and transversely flattened; however, it is transversely thicker posteriorly rather than anteriorly. The anterior margin is sharp, whereas the posterior margin of the neural spine is thickened.

The most posterior dorsal vertebra preserved (CMP-MS-04-06) (Figure 2G–I) is approximately the last of the series (probably d16) based on the shape of the centrum and comparisons with *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* [24,25]. The morphology of the centrum is similar to that of CMP-MS-04-02, but the articular facets and the neural canal are relatively larger than the aforementioned vertebra. In addition, a subtle and narrow midline keel is present in the ventral surface of this centrum. The prezygapophyses are incomplete anteriorly and the only recognizable element of the neural arch. Its oval facets are large and ventromedially directed forming an angle of approximately 145 degrees between them as in CMP-MS-04-02. Differing from the latter, the separation between both prezygapophyses is relatively longer.

A fragmentary dorsal or sacral neural spine (CMP-MS-04-18) is preserved (Figure 2J–L). The neural spine is anteroposteriorly expanded and transversely thicker posteriorly rather than anteriorly. The anterior margin is sharp, whereas the posterior margin of the neural spine is thickened with a shallow central groove. Despite incomplete the preserved fragment of neural spine is parallel-sided (Figure 2K). All the preserved surfaces of the fragmentary neural spine are heavily rugose.

3.2.2. Sacrum

The preserved sacrum consists of eight firmly co-ossified sacral vertebrae recovered in three blocks (Figure 3A–C). The sacrum is straight along its length when is viewed laterally. All the sacral centra are complete with exception of the sacrodorsal centrum, of which the mid-ventral portion is not preserved (Figure 3D). Portions of the transverse processes, sacral ribs and neural spines are preserved in most of the true sacral vertebrae (Figure 3A–C). The first vertebra corresponds to the sacrodorsal; therefore, the sacrum is composed of seven true sacral vertebrae (Figure 3A). Only the large prezygapophyses are preserved in the neural arch of the sacrodorsal vertebra. The surface of the prezygapophyses is almost flat and subovoidal. The prezygapophyses are slightly extended beyond the anterior margin of the centrum.

The centrum of the first true sacral is axially short compared to succeeding sacral vertebrae and its present expanded anterior and posterior articular facets. The preserved axially short and transversely broad base of the neural spine of sacral 1 is fused to that of the sacral 2. The ventral surface of this first true sacral vertebra presents a broad rounded keel.

The succeeding sacral vertebrae, from sacral 2 to 6, present centra that become progressively broader and massive. A narrow midline ventral keel is present in sacral 2, whereas a broad midline ventral sulcus is developed in sacral 3 to 6. However, in sacral 3 the sulcus is restricted to the posterior half of the centrum. In all these vertebrae, the sacral ribs are clearly positioned in the intercentrum position as in sacral 1. When preserved (sacral 3 to 6) the sacral ribs are firmly fused to the transverse processes.

These transverse processes are horizontally directed. Despite broken, the bases of the neural spines of sacral 3 to 5 are fused to each other. The ventral surface of the centra in sacral 2 and 3 is gently convex, whereas in sacral 4–6 a shallow longitudinal sulcus is developed in their ventral centrum surfaces (Figure 3C). The last of the true sacral vertebrae is the largest. Its posterior articular facet is large, circular and slightly concave, whereas its ventral surface is heavily eroded. Despite broken at their bases the transverse processes and sacral ribs are positioned in the intercentrum position.

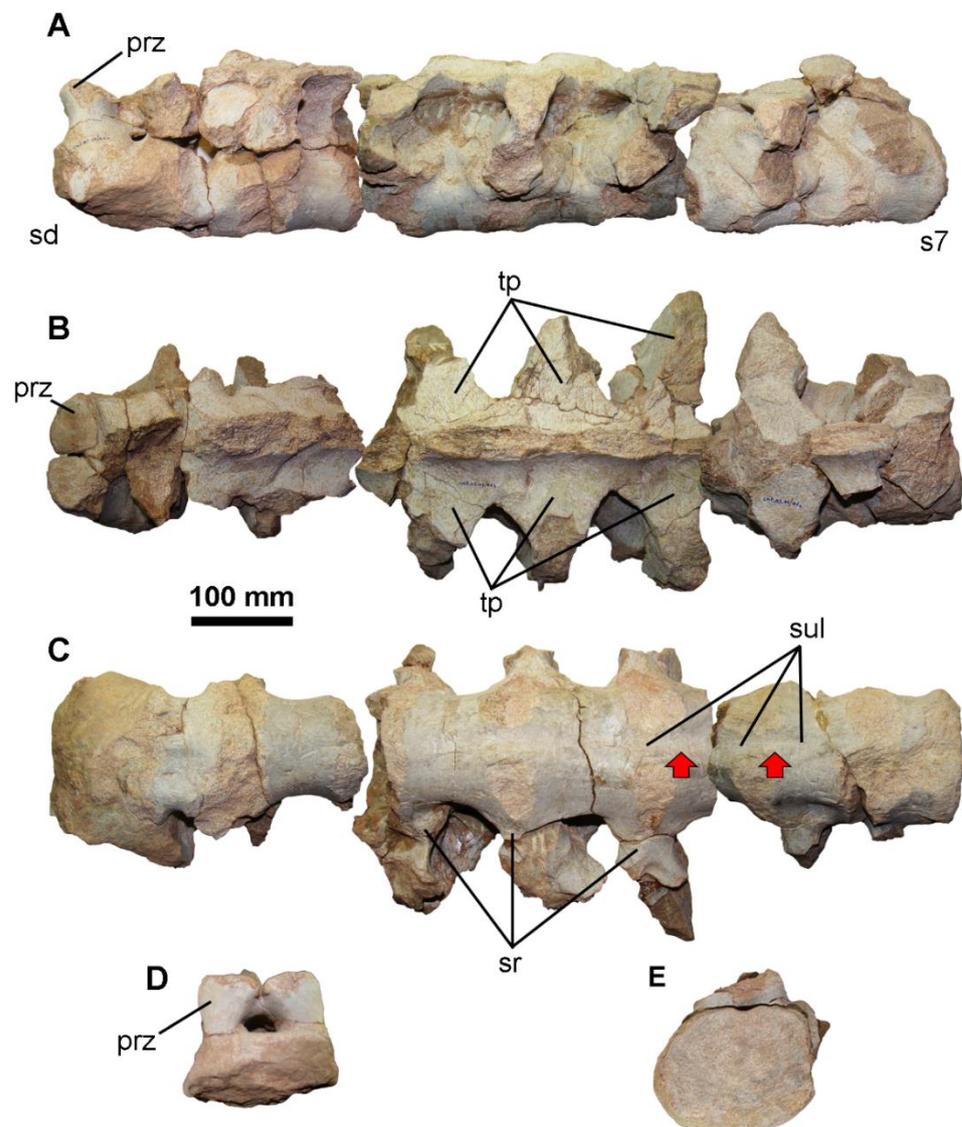


Figure 3. Sacrum of the specimen CMP-MS-04. CMP-MS-04/01 in left lateral (A), dorsal, (B), ventral (C), anterior (D), and posterior (E) views. Abbreviations: prz, prezygapophysis; sd, sacrodorsal vertebra; sr, sacral ribs; sul, midline sulcus; s7, sacral vertebra 7; tp, transverse process. Red arrows mark the distinctive character that assigned the specimen CMP-MS-04 to *Iguanodon bernissartensis*.

3.2.3. Caudal Vertebrae

Three incomplete caudal vertebrae (CMP-MS-04-03, -04, and -07) and a mid-caudal centrum (CMP-MS-04-05) are preserved (Figure 4). Both CMP-MS-04-03, -04, and -07 are considered anterior caudal vertebrae based on the presence of transverse processes which disappear posterior to the c14 in *Iguanodon bernissartensis* [24] or c15-16 in *Mantellisaurus atherfieldensis* [25]. Based on its centrum size and proportions, CMP-MS-04-07 is the most anterior in the caudal series. The description of these vertebrae is here based on the most complete vertebra recovered, CMP-MS-04-03.

These vertebrae have the anterior articular facets of the centra flat, whereas the posterior articular facets are concave. Despite being broken, the transverse processes are in the dorso-lateral surface of the centra. The ventral surface of the centra is longitudinally concave between the margins of the haemal arch facets. The neural arches are low, robust, and slightly anteriorly positioned. The neural canal is almost circular and small in CMP-MS-04-03, whereas it is larger and oval with the large diameter transversely in

CMP-MS-04-04 and in CMP-MS-04-07. In the latter, the neural canal is almost circular but larger anteriorly than posteriorly.

The prezygapophyses are slightly extended beyond the anterior margin of the centra when they are totally preserved (Figure 4B,J). Their suboval facets are ventromedially directed and considerably separated. The postzygapophyses are located at the base of the neural spine and slightly extended beyond the posterior margin of the centra. The facets of the postzygapophyses are oval and ventromedially directed. A small spinopostzygapophyseal fossa (spof) is present between both postzygapophyses.

The neural spines are broken at level of their bases in CMP-MS-04-04 and CMP-MS-04-07, whereas is best preserved in CMP-MS-04-03. The neural spine is anteroposteriorly shortened (compared to those of the dorsals) and transversally flattened. The neural spine is posteriorly inclined and bears a midline ridge in the lower portion of the anterior margin, whereas the rest of the preserved anterior margin is thicker and the posterior margin is thickened.

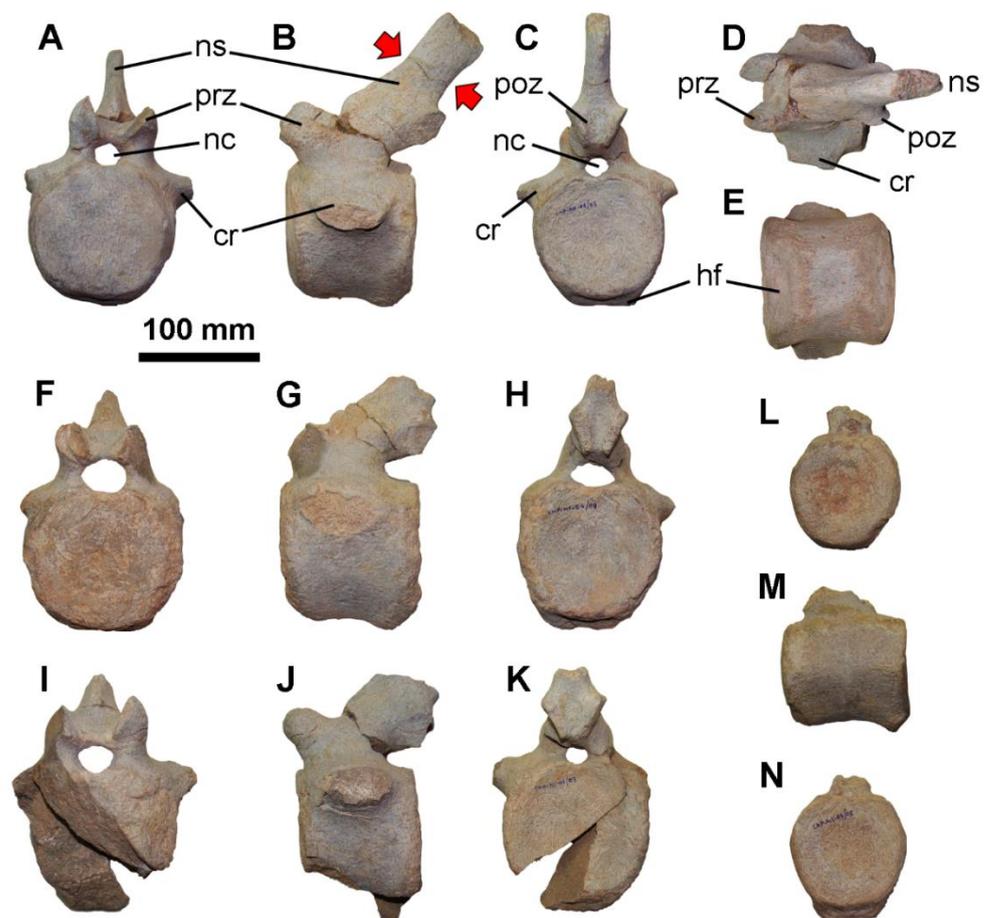


Figure 4. Caudal vertebrae of the specimen CMP-MS-04. CMP-MS-04/03 in anterior (A), left lateral (B), posterior (C), dorsal (D), and ventral (E) views. CMP-MS-04/04 in anterior (F), left lateral (G), and posterior (H) views. CMP-MS-04/07 in anterior (I), left lateral (J), and posterior (K) views. CMP-MS-04/05 in anterior (L), left lateral (M), and posterior (N) views. Abbreviations: cr, caudal rib; hf, haemal arch facet; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. Red arrows mark the distinctive character that assigned the specimen CMP-MS-04 to *Iguanodon bernissartensis*.

Based on its morphology and the absence of transverse processes CMP-MS-04-05 is a mid-caudal centrum (Figure 4L–N). The centrum is amphicoelous and elongate compared with those of the anterior caudal vertebrae. The transverse processes are absent but on both sides of the centrum there is a mid-height longitudinal reduced ridge. The centrum has a

ventral midline sulcus. The anterior and posterior articular facets of the centrum are almost hexagonal in profile.

There are two haemal arch facets on the anterior and posterior caudoventral surfaces of the centrum, respectively. However, the posterior haemal arch facet is larger and clearly more prominent than the anterior haemal arch facet. The preserved neural arch is low and anteriorly positioned. The narrow neural canal is almost circular in profile. The morphology of the caudal vertebrae of CMP-MS-04 resembles those of *Iguanodon bernissartensis* in having caudal vertebrae have parallel sided neural spines (Figure 4B).

3.2.4. Haemal Arches

Two nearly complete haemal arches (CMP-MS-04-09 and -10) (Figure 5A–F) and the proximal portion of other five (Figure 5G–M) are preserved. The proximal surface of these haemal arches is transversely expanded and bears two articular facets. Each articular facet is divided into a steeply inclined anterior portion and an almost horizontal posterior portion.

When they are preserved, a dorsoventrally elongate and large haemal canal is present, and the shaft of the haemal arch is straight and subcircular in section. In CMP-MS-04-10 (Figure 5D–F) the shaft is anteroposteriorly expanded having a posterior sharp margin. The fused articular facets and the morphology of the shaft in the case of CMP-MS-04-09 and -10 suggest that the haemal arches preserved may have been associated with anterior caudal vertebrae [26].

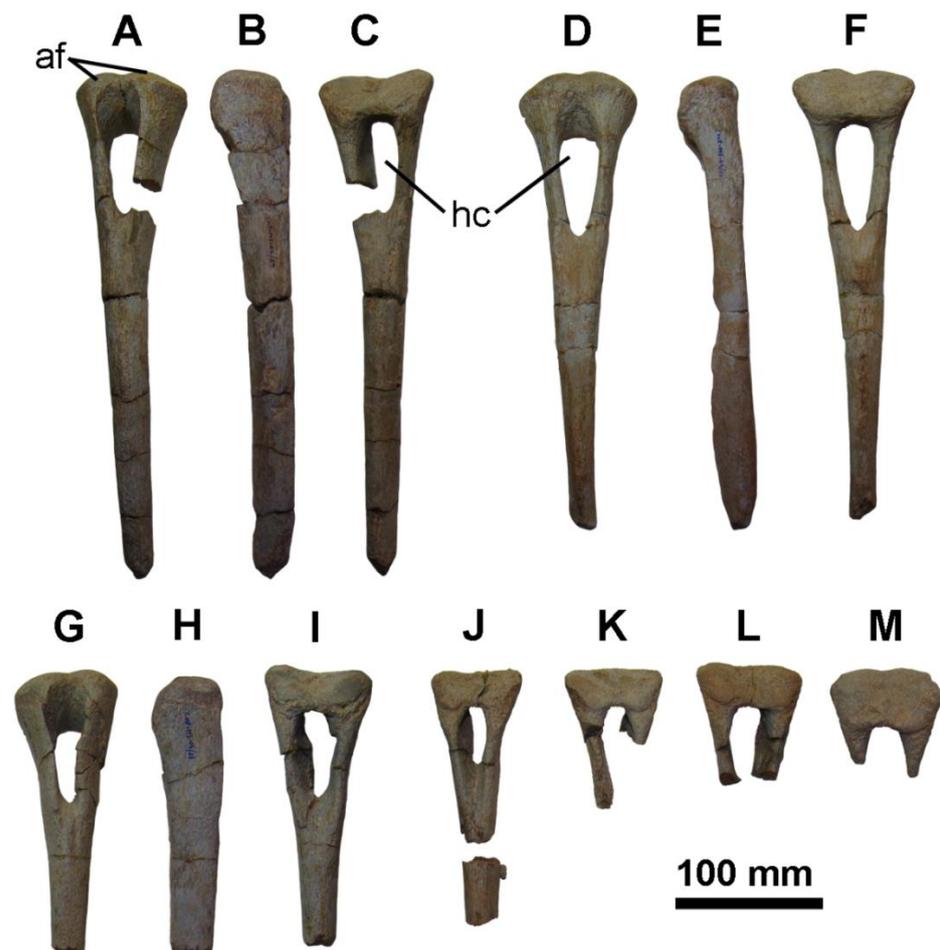


Figure 5. Haemal arches of the specimen CMP-MS-04. CMP-MS-04/09 in anterior (A), right lateral, (B), and posterior (C) views. CMP-MS-04/10 in anterior (D), right lateral, (E), and posterior (F) views. CMP-MS-04/11 in anterior (G), right lateral, (H), and posterior (I) views. CMP-MS-04/12–16 (J), CMP-MS-04/13 (K), CMP-MS-04/14 (L), and CMP-MS-04/15 (M) in posterior views. Abbreviations: af, articular facet; hc, haemal canal.

4. Discussion

Even though no histological analyses have been made, the degree of closure between the dorsal, sacral and caudal vertebral centra and their respective neural arches (when they are preserved) indicates maturity in CMP-MS-04. Furthermore, the presence of a sacrum with fused vertebrae is a feature that relates CMP-MS-04 with a mature specimen [10]. Based on the vertebral size and the comparison of the vertebrae with those of the type specimen of *Iguanodon bernissartensis* (IRSNB R51), an individual approximately 11 m in length [24,27], we estimate a similar length for the Mas de Sabaté individual.

4.1. Taxonomic Status of CMP-MS-04

Due to the incompleteness of the specimen, it has not been considered appropriate to try to discuss it in the framework of a phylogenetic analysis. However, an assessment of the taxonomic status of the specimen is established based on character comparisons within Ornithopoda.

Thus, six or more sacral vertebrae, eight in CMP-MS-04, is a feature commonly distributed among Cerapoda but shared with *Heterodontosaurus* and *Othnielosaurus* [28]. CMP-MS-04 can be assigned to Ankylopollexia based on the presence of dorsal neural spines that are taller than anteroposteriorly elongate [20]. A styracosternan affinity is suggested by the moderate opisthocoely of the mid-dorsal vertebra [20]. The presence of a tall and narrow mid-dorsal vertebra in addition to the posterior dorsal vertebra in which the centra are tall and broad with an almost circular, broadly heart-shaped posterior articular facet and opisthocoely increased in posterior dorsal are a unique combination of features of *Iguanodon* among the Early Cretaceous European styracosternan ornithopods [10].

These characters are shared by CMP-MS-04. In addition, a sacrum composed of eight sacral vertebrae is a potential autapomorphy of *Iguanodon* [10] and it is observed in CMP-MS-04. Within the genus parallel-sided neural spines in dorsal and caudal vertebrae and the presence of a ventral keel in posterior dorsal centra and a midline broad ventral sulcus in the more posterior sacral centra relates unambiguously CMP-MS-04 with *Iguanodon bernissartensis* [10].

4.2. Comparisons with Other Early Cretaceous Styracosternans

The morphology of the dorsal vertebrae of CMP-MS-04 resembles those of *Iguanodon* in having a tall and narrow mid-dorsal vertebra and a tall but broad posterior dorsal centra in which posterior articular facets are almost circular and broadly heart-shaped [10]. In *Mantellisaurus atherfieldensis* and *Morelladon beltrani* the dorsal series are characterized by having low cylindrical centra [11,25,29]. The absence of dorsal centra that are lean posteriorly and with unusually thickened articular rims distinguishes CMP-MS-04 from *Hypselospinus fittoni*. In addition, in posterior dorsals d14-15 of *Hypselospinus fittoni* a ventral keel is present and just d16 is characterized by having no ventral keel [20].

The posterior centra of CMP-MS-04 are similar to those of *Barilium dawsoni* in having an anteroposteriorly compressed centra and prominently expanded margins of the articular facets, in addition to their slightly developed opisthocoely. This combination of features is shared with *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis*. However, differing from those of CMP-MS-04 posterior dorsals d14-16 of *Barilium dawsoni* retain short ventral midline keels [26].

Similarly, the posterior dorsals d12-16 of *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* possess narrow ventral keels [24,25]. A ventral midline keel is also present in the coetaneous styracosternan *Morelladon beltrani* [11]. Regarding *Iguanodon galvensis*, the new information provided by DS-1 ornithopod ascribed as *I. cf. galvensis* indicates that the posterior dorsal vertebrae of this Iberian taxon can be distinguished from those of CMP-MS-04 by having moderately compressed centra between the articular facets and the absence of a ventral keel [12,15].

The neural spine is inclined caudally in middle and posterior dorsals of *Hippodraco scutodens* [30]. Middle and posterior dorsals of *Iguanacolossus fortis* possess dorsally taper-

ing neural spines [30] differing from the parallel-sided neural spines of *Barilium dawsoni*, *Hippodraco scutodens*, *Hypselospinus fittoni*, *Iguanodon bernissartensis*, *Iguanodon galvensis* and *Mantellisaurus atherfieldensis* or the more anteroposteriorly expanded distally than proximally neural spines of *Ouranosaurus nigeriensis* and *Morelladon beltrani* (middle dorsals) [11,31].

Despite being incomplete, the neural spine of CMP-MS-04 is parallel-sided (Figure 2E). Differing from the extremely tall and deep spinopostzygapophyseal fossa of the posterior dorsal neural spines of *Morelladon beltrani*, in CMP-MS-04 this fossa is also deep but small (Figure 2C,F) as in other styracosternans, such as *Barilium dawsoni*, *Hippodraco scutodens*, *Iguanacolossus fortis*, *Iguanodon bernissartensis*, *Iguanodon galvensis* and *Mantellisaurus atherfieldensis*.

As in *Iguanodon bernissartensis* [24,27,29], the sacrum of CMP-MS-04 specimen is characterized by the presence of eight co-ossified vertebrae. In *Ouranosaurus nigeriensis* and *Morelladon beltrani* the sacrum comprises six co-ossified vertebrae [11,31], whereas seven co-ossified sacral vertebrae are the number present in *Barilium dawsoni*, *Mantellisaurus atherfieldensis* and probably in *Hypselospinus fittoni* and *Lurdusarus arenatus* sacra [20,25,26,29,32]. As occurs in *Iguanodon bernissartensis* the sacrum of CMP-MS-04 specimen is characterized by having a broad ventral sulcus in the midline of the more posterior sacral centra.

This feature clearly distinguishes *Iguanodon bernissartensis* from other styracosternans, such as *Barilium dawsoni*, *Hypselospinus fittoni*, *Mantellisaurus atherfieldensis* or *Morelladon beltrani* (except in the last sacral vertebra that has a convex ventral surface) in which a midline keel is present [11,20,25,26] or *Ouranosaurus nigeriensis* in which the ventral surface is convex [31]. Nevertheless, a similar ventral sulcus is also present in the posterior sacral vertebrae of *Equijubus normani* [33] and *Proa valdearinnensis* [13]. Similarly, some authors [10,13] considered this feature might be susceptible of ontogenetic variation in the Iberian taxon *Iguanodon galvensis*. In this species, perinates individuals preserve articulated sacrum with no ventral sulcus [10], although sacra in mature specimens are unknown.

The morphology of the anterior caudal vertebrae of CMP-MS-04 resembles those of *Iguanodon bernissartensis* in having caudal centra that are platycoelus and parallel-sided neural spines (Figure 4B). In contrast, the anterior caudal centra of *Barilium dawsoni* and *Mantellisaurus atherfieldensis* are amphiplatyan, whereas, in *Jinzhousaurus yangi*, *Ouranosaurus nigeriensis* and *Yunganglong datongensis* [34], the centra are amphicoelus.

As in some adult specimens of *Iguanodon bernissartensis* a longitudinal ventral sulcus in the middle caudal vertebra is present in CMP-MS-04. However, the presence or absence of this sulcus is related to individual variation in *Iguanodon bernissartensis* and probably in *Mantellisaurus atherfieldensis* [27]. Furthermore, a longitudinal ventral sulcus has been reported in other styracosternans, such as *Dakotadon lakotaensis*, *Hypselospinus fittoni* or *Planicoxa venenica* [20,27,35,36].

As in most styracosternan ornithopods the articular facets of the haemal arches are fused differing from those of *Lurdusaurus arenatus* in which the articular facets are totally separated [37]. The best preserved haemal arches present straight shaft differing from the posteriorly curved and pointed shafts from the first three haemal arches of *Iguanodon bernissartensis* [24] and *Jinzhousaurus yangi* [38] or the first haemal arch of *Mantellisaurus atherfieldensis* [25] or the probably first haemal arch of *Morelladon beltrani* [11].

However most posterior haemal arches of the anterior series of *Iguanodon bernissartensis* [24], *Jinzhousaurus yangi* [38] and *Mantellisaurus atherfieldensis* [25] present straight shafts, whereas in *Iguanacolossus fortis* the shaft of a well-preserved anterior haemal arch curves posteriorly along its length [30]. In *Ouranosaurus nigeriensis*, the most anterior haemal arches are slightly posteriorly inclined, whereas middle haemal arches present straight shafts [31].

4.3. Abundance and Diversity of the Dinosaur-Bearing Deposits of the Arcillas de Morella Formation

The Arcillas de Morella Formation is an upper Barremian unit within the Morella sub-basin (Maestrat basin) located in the north-eastern of the Iberian Peninsula [5,23]. Among the more than 40 vertebrate fossil sites documented in this formation Mas de la Parreta quarry (CMP) is particularly noteworthy (Figure 6) [5]. In this area, twenty dinosaur-bearing fossil sites have been documented thus far. Additionally to the dinosaur remains, the vertebrate fossil community is composed by teleosteans fishes and sharks, pleiososaurs (including an indeterminate leptocleidid [39]), turtles (at least the dortokid *Eodor-toka morellana* [40], a solemydid and the xinjiangchelyid *Brodiechelys royoi* [41]), neosuchian crocodyliforms (atoposaurids, bernissartiids and goniopholidids) and pterosaurs [5].

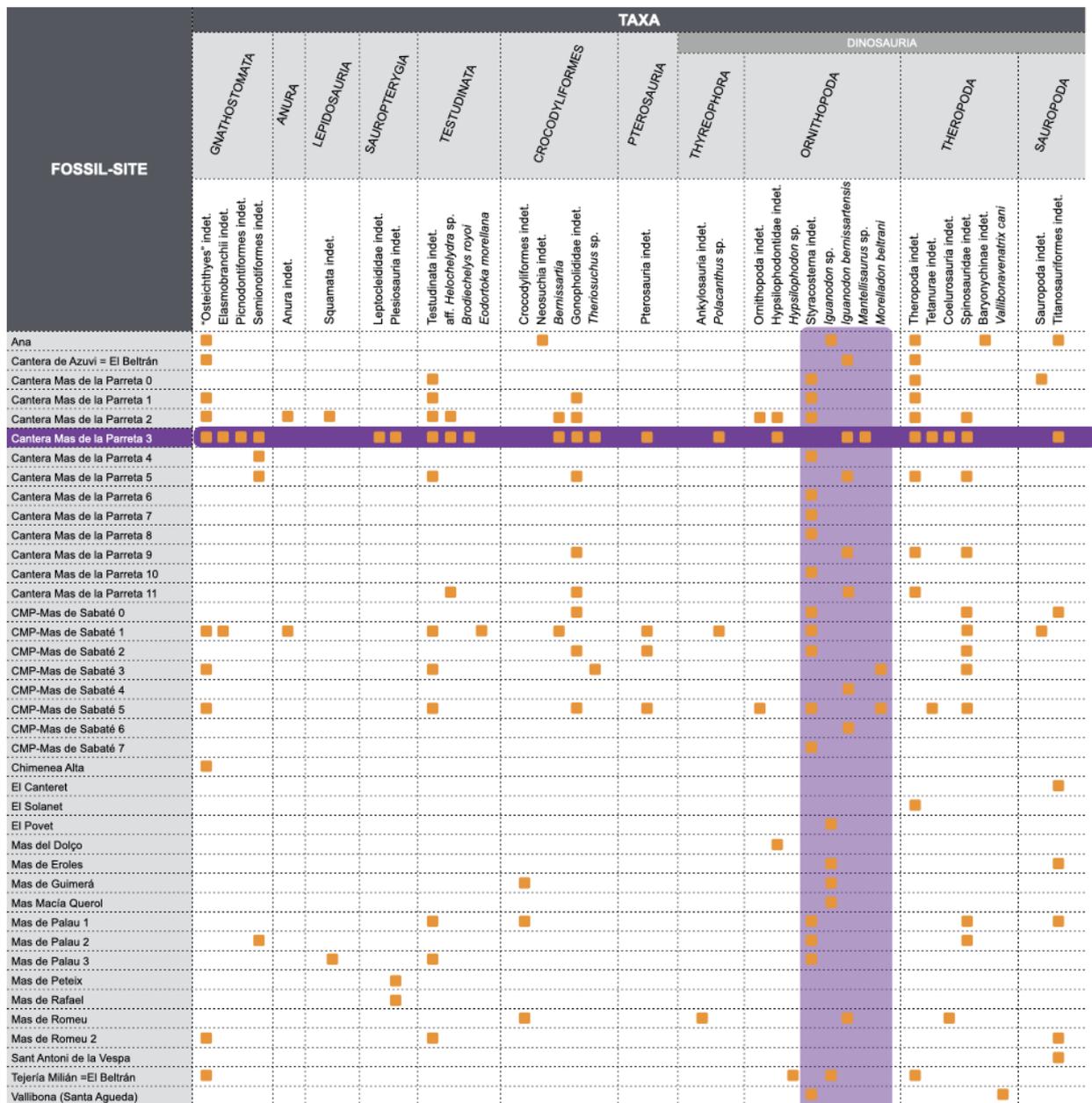


Figure 6. List of the vertebrate fauna recorded from the beds of the Arcillas de Morella Formation ([5] and references therein, [39,42,43]). Dark purple indicates Mas de la Parreta quarry site 3, whereas light purple indicates non-hadrosaurid styrcosternan occurrences in the formation.

The dinosaur record currently recognized at the CMP quarry includes at least one indeterminate titanosauriform sauropod; allosauroid, coelurosaur and spinosaurid (including *Vallibonavenatrix cani*) [42,43] theropods; the ankylosaur *Polacanthus* [44]; an indeterminate hysilophodontid; and non-hadrosaurid styracosternan ornithopods [5]. Among this diverse fauna, it is worth highlighting the discovery of more than 2,000 non-hadrosaurid styracosternan ornithopod dinosaur remains, including some partial skeletons of distinct medium- to large-sized individuals. To date, three non-hadrosaurid styracosternan species are recognized in the CMP quarry: *Iguanodon bernissartensis*, *Mantellisaurus atherfieldensis* and *Morelladon beltrani* [5–9,11].

To date, the higher vertebrate diversity is located at the Mas de la Parreta quarry CMP-3 site (Figure 6). In this site, fossil remains are distributed into coastal and shallow-marine bioclastics above the transgressive surface that separate continental red clays and sandstones from the sandy limestones. Here, the accumulation of both terrestrial and marine fauna, even flora, is remarkably high and it is related to punctuated episodes of coastal to marine influence [23].

Based on the number of localities in which each vertebrate group occurs (Figure 6), non-hadrosaurid styracosternan ornithopods are by far the group of vertebrates most frequently recorded in the formation. Interestingly, in all the twenty fossil sites of the Mas de la Parreta quarry (CMP) non-hadrosaurid styracosternan fossils remains have been documented. The number of taxa within different dinosaur groups in the Arcillas de Morella Formation clearly indicates that the greatest diversity occurs both among ornithopods and theropods.

As mentioned above, three non-hadrosaurid styracosternan species and at least one indeterminate hysilophodontid composed the known ornithopod palaeocommunity. Both ankylosaur and sauropods are the less diverse group of dinosaurs in this Early Cretaceous unit. In the case of sauropods, some authors consider that the titanosauriforms diversity is higher [45] in the formation; however, further analysis is needed to better understand the sauropod diversity.

Among the non-dinosaurian vertebrate fauna reported in the Arcillas de Morella Formation, neosuchian crocodyliforms and turtles are the most diverse. For these non-dinosaurian vertebrate groups, their diversity is similar to that of theropods but higher than ankylosaurs and sauropods. Only ornithopods show a higher diversity than crocodyliforms and turtles.

Finally, the vertebrate assemblage recovered in the Arcillas de Morella Formation closely resembles those of other sedimentary deposits of the Wealden Group facies from northwest Europe [9], mainly the Barremian-lower Aptian deposits of the British upper Wealden and the Belgium Sainte-Barbe Clays Formation. As occur in these European Early Cretaceous strata [46,47] and other Iberian Early Cretaceous deposits [48] the faunal assemblage recovered in the Arcillas de Morella Formation is dominated by medium- to large-sized non-hadrosaurid styracosternan iguanodontians.

5. Conclusions

The most representative dinosaur group of the late Barremian Arcillas de Morella Formation are non-hadrosaurid styracosternan ornithopods, which are also very abundant throughout the Iberian Lower Cretaceous. Associated new ornithopod axial material from the upper Barremian Arcillas de Morella Formation in Eastern Spain have been described. Based on the unique combination of shared characters, the new specimen from Mas de Sabaté site can be confidently referred to *Iguanodon bernissartensis*.

These characters include the morphology (parallel-sided) of the neural spines in dorsal and caudal vertebrae and the presence of a ventral keel in posterior dorsal centra and a broad ventral sulcus in the midline of the centra ventral surface of the most posterior sacral vertebrae. Therefore, the presence of *Iguanodon bernissartensis* in the Arcillas de Morella Formation is herein confirmed. The new specimen can be regarded as a large-sized *Iguanodon bernissartensis* individual of an estimated body length of 11 m.

Even though *Iguanodon bernissartensis* remains are relatively common in Mas de la Parreta Quarry, this is the first evidence of this large bodied styracosternan dinosaur in the Mas de Sabaté site. To date, only the lightly built styracosternan *Morelladon beltrani* had been previously reported in this area.

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